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NOTES AND LITERATURE

LIFE HISTORIES IN THE RED ALGÆ

The past decade has given us a number of excellent life history studies in the *Rhodophyceæ* which have been of material assistance in clarifying a very difficult field in plant morphology. The more important of these contributions will form the subject of this review.

Yamanouchi[1] in 1906 published an account of the life history of *Polysiphonia violacea* based on cytological investigations of all of its significant phases. He arrived at the following chief conclusions: (1) Carpospores have 40 chromosomes and tetraspores 20, *i. e.,* half of this number. (2) The sexual plants in their vegetative mitoses showed 20 chromosomes and therefore were believed to arise from tetraspores. (3) The asexual or tetrasporic plants showed 40 chromosomes throughout their vegetative history and consequently could be assumed to come from carpospores. (4) The production on the asexual plants of tetraspores is the result of a reduction division since the first mitosis in the tetrasporangium is clearly heterotypic as shown by the characteristic pairing of the 40 chromosomes and the separation of the members of each pair; thus each tetraspore comes to have 20 chromosomes and is prepared to develop a sexual plant. (5) It was therefore clear that the formation of tetraspores determines the end of a sporophytic generation in the manner characteristic of plants. (6) The gamete nuclei of the sperms and carpogonia take the 20 chromosomes of the sexual plants and fertilization gives the zygote nucleus with 40 chromosomes. (7) Descendants from the zygote nucleus enter the carpospores which consequently have 40 chromosomes and on germination would give tetrasporic plants; certain complicated cell fusions during the development of the cystocarp are purely cytoplasmic in character and evidently nutritional in function. (8) ''There is thus an alternation of a sexual plant (gametophyte) with a tetrasporic plant (sporophyte) in the life history of *Polysiphonia,* the cystocarp being included as an early part of the sporophytic phase.''

Yamanouchi's contribution on *Polysiphonia* has in great measure been the inspiration and largely furnished the basis for the comparative studies that shortly followed. Lewis[2] in 1909 presented an investigation of *Griffithsia Bornetiana* which is in essential agreement with the conclusions of Yamanouchi that an alternation of sexual and tetrasporic plants occurs. From the zygote nucleus, containing 14 chromosomes, are derived the nuclei of the carpospores. The tetrasporic plants have 14 chromosomes and were assumed to come from carpospores. The first mitosis in the tetrasporangium is a reduction division so that 7 chromosomes enter the tetraspores and these were believed to produce sexual plants. Lewis, however, held that the sporophyte generation was represented by the sporogenous cells of the cystocarp and considered the tetrasporic plant to be a phase of an homologous alternation of generations even though it was clear that the tetrasporic plant led up to the critical period of chromosome reduction in the tetrasporangium. From a study of *Griffithsia corallina* Kylin[3] questions the accuracy of the details of nuclear structure and mitoses as given by Lewis and also his count of the chromosomes which in *G. corallina* appear to be as high as in *Polysiphonia.* Kylin describes and figures the reduction phenomena in the tetrasporangium of *Griffithsia* in substantial agreement with Yamanouchi and in an earlier paper gives a similar account for *Rhodomela virgata.*[4]

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[1] Yamanouchi, S., ''The Life History of *Polysiphonia violacea,*'' *Bot. Gaz.,* XLII, 401–449, 1906.

Extremely interesting are the results of experimental cultures made by Lewis[5] through which fruiting plants have been grown from sporelings established in the laboratory on oyster shells that were then favorably placed in the sea. From carpospores of *Polysiphonia violacea* 6 tetrasporic plants were developed and 23 sterile. Tetraspores of *Griffithsia Bornetiana* produced a total of 60 sexual plants (32 male and 28 female) and 15 sterile. Tetraspores of *Dasya elegans* gave 149 sexual plants (143 male and 6 female) and 139 sterile, the apparently large proportion of male plants in the culture of this species probably being due to slower maturing of the females. The sterile plants of these cultures were of course individuals which at the time of the examination had not yet developed fruiting organs. More extended studies of Lewis[6] have established the seasonal habits at Woods Hole, Massachusetts, of the above species of *Polysiphonia, Griffithsia* and *Dasya.* Tetraspores and carpospores were germinated on shells that were fastened to piles and left over winter. In June tetrasporic plants of carposporic origin were abundant, which, releasing their tetraspores in July, produced a crop of sexual plants that matured their carpospores in August or early September. The small plants from the carpospores winter over and produce the tetrasporic plants of the first summer generation. Thus the sexual generation is conspicuous in the late summer while tetrasporic plants surviving the winter are characteristic of the spring. Belated growth of tetrasporic plants may result in their fructification late in summer, so that a few small carposporic plants also winter with the tetrasporic but they are relatively scarce. The seasonal history is then in the main characteristic; tetrasporic plants appear in the spring and through their spores produce a summer crop of sexual plants, from the carpospores of which a generation of small tetrasporic plants in favorable situations carries the species through the winter. This experimental work thus supports at all points the conclusions of Yamanouchi based on cytological studies.

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[2] Lewis, I. F., "The Life History of *Griffithsia Bornetiana,*" *Ann. of Bot.,* XXIII, 639–690, 1909.

[3] Kylin, H., "Die Entwicklungsgeschichte von *Griffithsia corallina* (Lightf.) Ag.," *Zeitsch. f. Bot.,* VIII, 97–123, 1916.

[4] Kylin, H., "Studien über die Entwicklungsgeschichte von *Rhodomela virgata* Kjellm.," *Svensk. Bot. Tidskr.,* VIII, 1914.

[5] Lewis, I. F., "Alternation of Generations in Certain *Florideæ,*" *Bot. Gaz.,* LIII, 236–242, 1912.

The most important cytological work on life histories in the red algæ since the paper of Yamanouchi on *Polysiphonia* is that of Svedelius presented in studies on *Martensia, Delesseria, Nitophyllum* and *Scinaia.* Part of this work, described in the next paragraph, concerns the development of tetraspores in multinucleate tetrasporangia (*Martensia* and *Nitophyllum*). All of it supports to the fullest degree Yamanouchi's theory of alternation of generations in such species as have tetrasporic plants in their life histories. The work on *Scinaia* presents a most interesting hypothesis for the life histories of such red algæ as do not develop tetraspores.

The life history of *Delesseria sanguinea* is discussed by Svedelius[7] in three papers embodying cytological work of a high order. Tetrasporic plants have 40 chromosomes in their nuclei. This number is reduced by the first nuclear division in the tetrasporangium. During synapsis the 40 chromosomes become grouped to form 20 pairs, which become exceptionally clear in the stage of diakinesis. The first or heterotypic mitosis separates the members of the pairs, thereby halving the number and giving after the second mitosis 20 chromosomes to each of the tetraspores. Vegetative mitoses in the male and female plants show uniformly 20 chromosomes and it must be assumed that these sexual plants develop from tetraspores. The chromosomes are organized in the prophases of mitosis directly from a chromatic network and without the interpolation of a spirem stage. The spermatangia are cut off in pairs to the right and left of a mother cell and in each spermatangium a uninucleate sperm is organized (20 chromosomes) which on escaping leaves behind an empty cyst. The young carpogonium is uninucleate but an early division differentiates the female gamete nucleus (20 chromosomes) which remains in the carpogonium, and a trichogyne nucleus that shortly breaks down. The carpogonium terminates a 4-celled carpogonial branch borne by a cell ("tragzelle") from which develops also an auxiliary cell and certain sterile cells. The sterile cells enlarge greatly after the fertilization of the carpogonium and then break down, forming a mass of slime which apparently serves to give space and protection for the development of the gonimoblasts. In some way not clearly understood the zygote nucleus of the fertilized carpogonium enters the auxiliary cell and from this cell as a starting point the gonimoblasts arise as a dense growth of short filaments. The cells of the gonimoblasts contain nuclei derived from that of the zygote and consequently have 40 chromosomes which are passed on to the carpospores developed in rows. From the carpospores must come the tetrasporic plants with their 40 chromosomes. We have therefore in *Delesseria* an antithetic alternation of generations exactly parallel with that of *Polysiphonia,* a diploid phase including the gonimoblasts and the tetrasporic plants alternating with a haploid phase represented by the sexual plants.

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[6] Lewis, I. F., "The Seasonal Life Cycle of Some Red Algæ at Woods Hole," *Science,* XXXIX, 253, 1914.

[7] Svedelius, N., "Ueber den Generationswechsel bei *Delesseria sanguinea,*" *Svensk. Bot. Tidskr.,* V, 260–324, 1911. "Ueber die Spermatienbildung bei *Delesseria sanguinea,*" *ibid.,* VI, 239–265, 1912. "Ueber die Zystokarpienbildung bei *Delesseria sanguinea,*" *ibid.,* VIII, 1–32, 1914.

Svedelius[8] opened a new vista in cytological studies on the red algæ with his discovery of multinucleate tetraspore mother cells in *Martensia,* one of the *Delesseriaceæ.* The young cell has like its neighbors several nuclei which by division increase in number as the cell enlarges until about 50 are present. Then a general nuclear degeneration sets in coincident with an increase in the amount of cytoplasm and only one nucleus in the center of the plasma mass survives to give rise to the 4 nuclei that enter the tetraspores. A similar situation was found by Svedelius[9] in *Nitophyllum punctatum,* a related form of the same family, which is described in greater cytological detail. Typical mitoses in the young tetraspore mother cell give it a dozen or more nuclei all with about 40 chromosomes, the diploid number for the species. Many of the nuclei shortly begin to show signs of degeneration by the disappearance of the chromatin so that only the nucleolus remains to take the stain, and there is also a shrinkage of the nuclear membrane. The degeneration is not simultaneous, a few nuclei increase in size and give indications of preparation for the heterotypic mitosis as shown by clear stages of diakinesis. However only one nucleus carries the history of reduction further and thus becomes the surviving nucleus of the tetraspore mother cell, a nucleus very much larger than the degenerating structures that lie about it in the cytoplasm. At diakinesis pairs of chromosomes are clearly shown, about 20 in number. The members of the pairs are separated by the first mitosis which is therefore heterotypic and a reduction division as in *Polysiphonia, Griffithsia* and *Delesseria.* The second mitosis, homotypic, gives the four nuclei of the tetraspores, each with about 20 chromosomes. It is very interesting to note that the red algæ present illustrations of nuclear degeneration at a period of reproduction when it may be desirable to conserve the cytoplasm of a cell for a limited number of reproductive elements. This nuclear degeneration appears to be strictly analogous from a physiological point of view to that exhibited in the oogonia of *Vaucheria, Saprolegnia* and *Albugo,* in the sporangium of *Derbesia,* and in the oogonia of certain forms of the *Fucaceæ.*

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[8] Svedelius, N., "Ueber den Bau und die Entwicklung der Florideengattung *Martensia,*" *Kungl. Svensk. Vet.-akad. Handl.,* XLIII, No. 7, 1908.

With the cytological and experimental evidence in complete accord and so strongly in favor of the theory of an antithetic alternation of generations in those red algæ which have tetrasporic plants certain observations which at first thought appear to offer exceptions to this theory naturally take on a high degree of importance. The literature records a number of species which have been reported to bear tetrasporangia on sexual plants, facts which would be significant if it were established that such tetrasporangia were the seat of reduction divisions. Three of these species have been studied cytologically and there is good evidence that the reduction divisions are not present and that tetraspores are either not fully matured or that the "tetrasporangium" develops a monospore. Yamanouchi and Lewis in their studies found occasional sexual plants bearing what seemed to be tetrasporangia but in these cells the nucleus remained undivided in *Polysiphonia* or produced several nuclei in *Griffithsia* while cleavage furrows proceeded only a short distance into the cytoplasm. Svedelius[10] has reported on a cystocarpic plant of *Nitophyllum punctatum* bearing tetrasporangium-like structures. These cells were found around points in the thallus where procarps had been formed and only reached their fullest development when the procarps remained unfertilized. Their position on the thallus therefore indicated a close correlation with the nutritional physiology of the plant. These cells in their early history follow exactly the course of normal tetrasporangia in this species; there is a multiplication of nuclei and then a degeneration of all but one which takes its position in the center of the cell. The surviving nucleus does not divide but the entire protoplast slips out of the thallus as a uninucleate monospore. Since the cystocarpic plant was haploid a reduction division in this tetrasporangium-like cell would have been most irregular; it does not take place and the monospore in its chromosome count has the same value as a tetraspore. *Agardhiella* (*Rhabdonia*) *tenera* presents another problem brought forward by observations of Osterhout. Tetraspores of this plant sometimes germinate while still imbedded in the tissues of the parent with the further peculiarity that the tetrad group behaves as a unit so that all four cells enter into the formation of a sporeling. These epiphytic sporelings commonly become sexual plants, as would be expected from the germination of tetraspores. Osterhout, however, reports that occasional tetrasporic plants are developed which would be irregular unless it were found that such plants came from tetrasporangia in which reduction divisions had been suppressed so that such tetrasporangia, behaving like monospores, give rise to diploid plants (tetrasporic) similar to the generations on which they were borne. It is probable that other red algæ will exhibit peculiarities of life history related to apospory, as seems probable in this case of *Agardhiella.*

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[9] Svedelius, N., "Ueber die Tetradenteilung in den vielkernigen Tetrasporangiumanlage bei *Nitophyllum punctatum,*" *Ber. deut. bot. Gesell.,* XXXII, 48–57, 1914.

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[10] Svedelius, N., "Ueber Sporen an Geschlechtspflanzen von *Nitophyllum punctatum;* ein Beitrag zur Frage des Generationswechsels der Florideen," *Ber. deut. bot. Gesell.,* XXXII, 106–116, 1914.

There is enough evidence before us in these three studies by Yamanouchi, Lewis and Svedelius to demand the utmost caution in the consideration of other cases of "tetraspores" upon sexual plants which have been brought forward by critics of the theory of alternation of generations as applied to the red algæ, cases which have not as yet been subjected to the tests of cytological research. One of the most interesting of these is *Platoma Bairdii* (Farl.) Kuckuck[11] which in Helgoland apparently produces no antheridia but develops cystocarps parthenogenetically. On these cystocarpic plants are also found tetraspores indicating that the plants are diploid in character which if true would account for their apogamous behavior. *Platoma Bairdii* therefore appears to be one of the cases in which sexual organs are developed upon a diploid plant and not one in which tetraspores are found on a haploid generation. A cytological study of this form would be a matter of great interest and the only way in which the facts may be determined. Also, there are the problems of the paraspores or polyspores characteristic of a number of species in the *Ceramiaceæ.* These are spores borne numerously in chains (seirospores) or in dense glomerules and are found on tetrasporic plants. Schiller[12] regards them as homologous with tetraspores, and as supporting the view of Oltmanns that the latter are reproductive spores without significance for an alternation of generations, but until we know the cytology of their development an opinion can have little value. Should the paraspores be formed without reduction divisions, as seems probable, they will rank in the same class with monospores and play no part in an alternation of generations. Should there be found evidence of a heterotypic mitosis in the development of these exceptional reproductive cells they might perhaps constitute a modification of the tetrad group characteristic of reduction divisions, but it does not seem likely that this will prove to be the case.

There is left for consideration those red algæ which produce no tetraspores at any phase of their life history. They include a number of well-known types such as *Nemalion, Batrachosper-*

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[11] Kuckuck, P., "Ueber *Platoma Bairdii* (Farl.) Kck.," *Wiss. Meeresuntersuch. Biol. Anstalt Helgoland.,* V, 187–203, 1912.

[12] Schiller, J., "Ueber Bau, Entwicklung, Keimung und Bedeutung der Parasporen der Ceramiaceen," *Oester. bot. Zeitsch.,* LXIII, 144, 203, 1913.

mum, Scinaia, Helminthora, etc., and at present constitute the field where research is most needed in connection with the life histories of the red algæ. Apart from asexual monospores the reproduction takes place only through carpospores produced in simple cystocarps. There are in the life histories no groups of tetrad cells to suggest the position of reduction divisions which explains the reasons why our understanding of alternation of generation in the *Rhodophyceæ* has come chiefly through higher forms exhibiting the tetrasporic phase. The first cytological research on a life history among the forms lacking tetraspores was the study by Wolfe[13] of *Nemalion.* This investigation brought out a number of important discoveries: the presence of a nucleus in the trichogyne, the mitosis which gives two sperm nuclei after the fusion with the trichogyne, the proliferation of the cells terminating the sporogenous filaments of the cystocarp to form successive carpospore mother cells, the structure of the chromatophore. With respect to the chromosome count in the life history Wolfe concluded that vegetative mitoses presented about 8 chromosomes and that 16 is probably the number shown by the mitoses in the developing cystocarp. The period of chromosome reduction was placed in the terminal cells of mature sporogenous filaments, one of the daughter nuclei, following a reduction mitosis, passing into a carpospore mother cell. The other reduced daughter nucleus was assumed to become established in the cell from which successive carpospores are produced by proliferation. The cytology of *Nemalion* is admittedly difficult and in the absence of a conspicuous group of four nuclei characteristic of reduction divisions (such as is found in the tetraspore mother cell) it is natural that critics of Wolfe's conclusions should have suggested other possible positions in the life history for the critical period of chromosome reduction. Thus it was suggested that reduction might take place at the germination of the carpospore, but Lewis[14] in a short note reports that the first and later mitoses in the sporelings are vegetative mitoses with about 8 chromosomes. A second possibility, that reduction takes place in the first division of the zygote nucleus in the fertilized carpogonium, is strongly debated by Svedelius in his recent paper on *Scinaia.*

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[13] Wolfe, J. J., "Cytological Studies on *Nemalion,*" *Ann. of Bot.,* XVIII, 607–630, 1904.

[14] Lewis, I. F., "The Germination of the Spore of *Nemalion multifidum,*" *Science,* XXXV, 154, 1912.

Svedelius[15] gives a cytological study of *Scinaia furcellata* which suggests some fundamental readjustments of our conception of the cystocarp in those red algæ which lack the tetrasporic phase in their life histories. Monosporangia and spermatangia occur on the same plants growing out of and becoming cut off from mother cells at the surface of the thallus with evidence that successive crops may be formed from the same mother cells. Both monosporangium and spermatangium have a nucleus with about 10 chromosomes and the similarity of their structure and manner of development indicates that they are homologous organs. The 3-celled carpogonial branch requires a somewhat detailed account since its history presents phases not previously described for the red algæ. The terminal cell becomes the carpogonium and a mitosis gives a nucleus to the trichogyne as has been described for *Batrachospermum, Nemalion, Polysiphonia, Rhodomela, Delesseria* and *Griffithsia.* From the second or hypogenous cell is formed a group of 4 auxiliary cells rich in protoplasmic contents. The third or basal cell of the carpogonial branch develops finally the envelope of the cystocarp. The nuclei of the carpogonial branch including the female gamete nucleus in the carpogonium have 10 chromosomes which is the haploid number of the *Scinaia* plant. After the fertilization of the carpogonium the zygote nucleus, with 20 chromosomes, and consequently diploid, passes into one of the auxiliary cells which have become more or less fused together. In the auxiliary cell the large zygote nucleus prepares for and passes through a heterotypic mitosis with apparently clear evidence of diakinesis shown in the presence of 10 pairs of chromosomes. A second mitosis gives the tetrad of 4 nuclei but only one of these becomes concerned with the development of the gonimoblasts, passing back into the carpogonium from which the gonimoblasts arise. The other 3 homologous nuclei of the tetrad together with the nuclei of the auxiliary cells take no further part in the history of the cystocarp. Nuclei of the gonimoblasts have 10 chromosomes and this number is passed to the carpospores which are formed successively in rows; some of the gonimoblasts remain sterile and develop into long filaments resembling paraphyses.

A most unexpected outlook upon the life histories of the red algæ will be opened if these conclusions of Svedelius on *Scinaia* are confirmed and if studies on *Nemalion, Batrachospermum,* etc., should also determine the position of chromosome reduction to be at the first mitosis of the zygote nucleus. The cystocarps of these plants would then be interpreted not as a diploid sporophyte generation but as a special haploid phase and the carpospores would have the same value as monospores. There would be no antithetic alternation of generations in such forms of the red algæ. Svedelius proposes the term *haplobiontic* for red algæ with this type of life history to be contrasted with *diplobiontic* forms (*Polysiphonia, Rhodomela, Griffithsia,* and *Delesseria*) where the gonimoblasts have been shown to be diploid in character and chromosome reduction finds its place in the terasporangia of an asexual generation. The diplobiontic type of life history is naturally conceived by Svedelius to arise from the haplobiontic by a delaying of the reduction divisions so that gonimoblasts carry forward the diploid number of chromosomes to the carpospores. The carpospores being diploid develop an asexual generation and their diploid sporangia becoming the seat of the reduction divisions take the characters of tetrasporangia, a new type of reproductive organ. The occasional suppression of reduction divisions in the tetrasporangium may be expected at times to transform this cell to a monosporangium, as in *Nitophyllum,* showing close analogies between the two structures.

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[15] Svedelius, N., "Zytologisch-Entwicklungsgeschichtliche Studien über *Scinaia furcellata,*" *Nov. Act. Reg. Soc. Scien. Upsal.,* IV, No. 4, 1915.

In connection with the conclusions of Svedelius on *Scinaia* it should be remembered that Allen has placed the reduction period in the life history of *Coleochæte* at the first mitosis of its zygote nucleus. If this view is correct the cellular body developed in the oospore of *Coleochæte,* preliminary to the formation of a crop of zoospores, is a special haploid structure and may be compared with the gonimoblastic development in *Scinaia* as interpreted by Svedelius. The haplobiotic red algæ of Svedelius then, if clearly established, would have the same type of life history as *Coleochæte* and bearing in mind the resemblance of the young oogonium of *Coleochæte* to a carpogonium and trichogyne, the resemblance of its antheridia to a cluster of spermatangia and the branched filamentous structure of its thallus, the view that *Coleochæte* represents a type from which the red algæ might have arisen takes on added strength.

It is interesting to note how far removed from the theories of Schmitz and Oltmanns are the more recent interpretations of the life histories in the red algæ. The secondary or double fertilization assumed by Schmitz as an explanation of the union of ooblastema filaments with auxiliary cells was discredited by Oltmanns's work and has received no support from the cytological studies of Yamanouchi, Lewis, Kylin and Svedelius. Oltmanns's view that tetraspores have no fixed place in ontogeny and are without relation to a sporophyte generation has been overwhelmed by the cytological work of the authors mentioned above. And now Svedelius argues that even the old view that cystocarps represent a sporophytic phase can not be correct for a group of the red algæ which he terms haplobiotic. The situation as it now stands may be summarized as follows: An antithetic alternation of generations may be expected wherever tetrasporic plants are found in a life history and in these forms the gonimoblasts also constitute a phase of the sporophyte. There is no sporophyte in the "haplobiotic" red algæ (*e. g., Scinaia* with *Nemalion, Batrachospermum,* etc., not yet studied from this standpoint) and the gonimoblasts of these forms represent a haploid development of the zygote in position upon the plant, carpospores being equivalent to monospores. Fusions with auxiliary cells are merely cytoplasmic in character and associated simply with nutritive functions. The diplobiotic red algæ have come from the haplobiotic, which, carrying forward the reduction divisions through the gonimoblasts and carpospores to a new generation, the tetrasporic plants, have established the reduction divisions in the tetrasporangium. In theory these views are simple and logical. For the antithetic alternation of sexual and tetrasporic plants the evidence is considerable and convincing. What will be the conclusions for the "haplobiotic" types? Will future studies establish their existence?

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